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THE REAPPEARANCE IN THE OFFSPRING OF ARTIFICIALLY PRODUCED PARENTAL MODIFICATIONS[1]

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In a recent paper[2] I have described a series of experiments conducted during the past few years upon white mice. I have there shown that large enough differences of temperature, operating throughout the period of growth, bring about considerable, and in some cases quite obvious, differences in the length of peripheral parts (tail, foot and ear), and probably changes in the quantity of hair as well. The peripheral parts were found to be longer in the warm-room lots (12 to more than 30 per cent. longer, in the case of the tail); the amount of hair, on the contrary, was less. It was pointed out, furthermore, that differences of precisely this sort have long been known to distinguish northern from southern races of mammals.

The question of most vital interest was not, however, touched upon in the earlier paper, although it has furnished my real motive for pursuing these experiments throughout. Are these modifications purely transitory, that is to say confined to the generation immediately affected, or do they reappear, if only to a slight degree, in the offspring? I have long felt that satisfactory evidence for or against the transmission of such modifications would be lacking, so long as zoologists confined themselves to a search for directly visible *qualitative* differences. With few exceptions, however, such has been the method by which the problem has been attacked.

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[1] This rather cumbersome title has been chosen in order to forestall any possible misrepresentation of my claims by those who do not read beyond headlines. Note that I have used the word "*reappearance,*" rather than "*inheritance.*"

[2] *Journal of Experimental Zoology,* August, 1909.

The following conditions must, I believe, be realized before we may hope to attain to any satisfactory test of this time-honored question: (1) We must select for experiment such an organism and such a physical agency that the latter may modify the former without directly influencing the germ cells. The action of temperature upon a warm-blooded animal seems to realize this condition most fully. (2) We must discover readily measurable, *quantitative* changes in the parent generation, before we can hope to test the reappearance of such changes in the offspring.

Having discovered such modifications in the parent generation, there are theoretically two methods by which we may attack the problem in hand. We may either (1) raise the offspring of the experimental and control[3] lots under identical conditions, or (2) we may raise the offspring of the modified parents under the same conditions as were employed to effect the original modification. In the first case, we should compare the two sets of animals having different parentage. Assuming a given modification of the value x, and supposing that $1/n$ represented the proportional part of this to be transmitted, the offspring of the two lots would be found to differ by the quantity x/n. If the second method were employed, we should compare the second generation with the parent generation, the two being measured at the same age.

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[3] For the sake of simplicity I have here assumed that one lot was merely a "control" lot, *i. e.*, exposed to normal or indifferent conditions. In my own experiments, however, I have chosen conditions with a view to modifying both sets of individuals in opposite directions.

Assuming that the latter had been modified to the extent x, the former, according to hypothesis, would be found to be modified to the extent $x + x/n$; *i. e.*, the effect of the conditions would have been cumulative.

Now, as a matter of fact, I have attempted both of these tests upon rather a large scale; but I have not yet found the second one to be practicable, owing to the difficulty, without special facilities, of repeating precisely the same temperature conditions during the lives of two successive generations. But the first test proved to be practicable, and has yielded the results which are summarized in the ensuing paper. Since the full data are to be published elsewhere in the course of the coming year, the omission of certain important portions of the evidence will, I trust, be condoned.

The parents of the mice to be discussed had been divided, at the commencement of life, into two lots, which were reared in separate rooms, differing widely in temperature.[4] Prior to the time of the pairing, they had been exposed to these conditions for an average period of about six months. For reasons which I shall not here state, the two contrasted groups ("warm" and "cold" lots) were not transferred to a common room before pairing.[5] Indeed, the females were not removed to such a room until the time that each was discovered to be pregnant. The discovery was made, on the average, about five days before the birth of the young, *i. e.*, about two weeks after the actual commencement of pregnancy. This circumstance is of possible importance in interpreting the results obtained. On that subject, more anon.

From the time that pregnancy became apparent, the mothers of the two lots were kept in the same room and under conditions which were identical, so far as care could make them so. Differences of temperature were particularly guarded against.

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[4] Differing by at least 15° C., on the average. The exact figures are not yet computed.

[5] The differences in temperature between the two experimental rooms were, however, very much reduced at this time.

The young were measured at the age of forty-two days. It was found to be impracticable to make certain of these measurements satisfactorily without subjecting the animals to ether. They were not, however, killed at this time. The weight, and the length of tail, foot and ear were determined. The linear measurements were taken with a graduated sliding caliper, indicating tenths of a millimeter. In the case of foot and ear, two measurements were made of each, the mean figure being employed in the computations.[6]

Of these mice, 286 survived to the age of six weeks; there being 141 offspring of warm-room parents, belonging to 33 litters, and 145 offspring of cold-room parents, belonging to 30 litters. From this earlier series of measurements the following gross averages were obtained:

	Weight (grams)	Tail (mm.)	Foot (mm.)	Ear (mm.)
Cold-room descendants	10.897	71.04	17.833	12.434
Warm-room descendants	10.631	71.19	17.960	12.536

It will be seen at once that, although the offspring of the warm-room mice average slightly less in weight, they have slightly longer tails, feet and ears than the offspring of the cold-room mice. These differences are exactly such as were noted, on a larger scale, in the parent generation. But such gross averages do not, in themselves, mean very much. In each of the contrasted groups are comprised individuals of widely different size (the extremes were 6.5 and 19.3 grams). Our material, therefore, is not at all homogeneous.

Accordingly, I have divided the animals into groups, comprising individuals of approximately the same weight.[7] Herewith are presented in tabular form the results of such an analysis.

From the table it will be seen that there are eleven groups in which a comparison between warm-room and cold-room descendants is possible. The mean tail length for the former animals is greater in eight of these eleven cases (exceptions starred); the mean foot-length is greater in nine of the eleven cases; while the mean ear length is greater in nine cases, and equal in one case. Let us consider the likelihood that such results have been obtained through "chance." What are the probabilities that, in tossing a coin, we shall throw "heads" or "tails" as many as eight times out of eleven? The chances that we shall obtain as great an excess as this (on one side or the other) are about 5 out of 22. This is admittedly not a very unlikely happening. The chances that nine of the eleven will be of one kind are about 1 in 15.

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[6] The average difference between the first and second reading of the caliper was 0.19 mm. for the foot, and 0.12 mm. for the ear.

[7] In my complete table I have likewise dealt with the sexes separately. Lack of space prevents this procedure here.

Group.	Parentage.	Number of individuals.	Weight.	Tail.	Foot.	Ear.
6–6.9 gms.	Cold	2	6.55	59.00	16.950	11.900
	Warm	3	6.77	60.67	16.800*	11.850*
7–7.9 gms.	Cold	12	7.57	61.91 ±0.79	16.954 ±0.110	11.850 ±0.076
	Warm	16	7.58	65.37 ±0.51	17.319 ±0.082	12.037 ±0.047
8–8.9 gms.	Cold	9	8.51	64.78 ±1.23	17.356 ±0.110	12.217 ±0.054
	Warm	19	8.48	67.11 ±0.45	17.642 ±0.052	12.313 ±0.054
9–9.9 gms.	Cold	23	9.41	68.65 ±0.57	17.572 ±0.069	12.311 ±0.035
	Warm	18	9.51	71.29 ±0.30	17.906 ±0.041	12.533 ±0.034
10–10.9 gms.	Cold	32	10.51	71.47 ±0.39	17.962 ±0.069	12.491 ±0.037
	Warm	27	10.33	70.41*±0.47	17.931*±0.050	12.559 ±0.043
11-11.9 gms.	Cold	27	11.42	73.62 ±0.36	17.975 ±0.063	12.534 ±0.0 5
	Warm	17	11.38	73.06*±0.38	17.994 ±0.057	12.568 ±0.085
12–12.9 gms.	Cold	16	12.46	73.37 ±0.66	17.844 ±0.100	12.544 ±0.065
	Warm	18	12.39	73.67 ±0.42	18.122 ±0.052	12.783 ±0.053
13–13.9 gms.	Cold	14	13.31	74.54 ±0.79	18.200 ±0.094	12.629 ±0.069
	Warm	12	13.32	76.33 ±0.46	18.504 ±0.052	12.842 ±0.083
14–14.9 gms.	Cold	3	14.30	75.67	18.333	12.617
	Warm	2	14.20	77.00	18.725	12.700
15–15.9 gms.	Cold	2	15.25	79.00	18.825	12.750
	Warm	6	15.40	77.33*	19.000	13.067
16–16.9 gms.	Cold	3	16.20	79.33	19.100	13.050
	Warm	3	16.37	83.00	19.217	13.050*
19–19.9 gms.	Cold	1	19.30	89.00	19.700	13.200
	Warm	0				

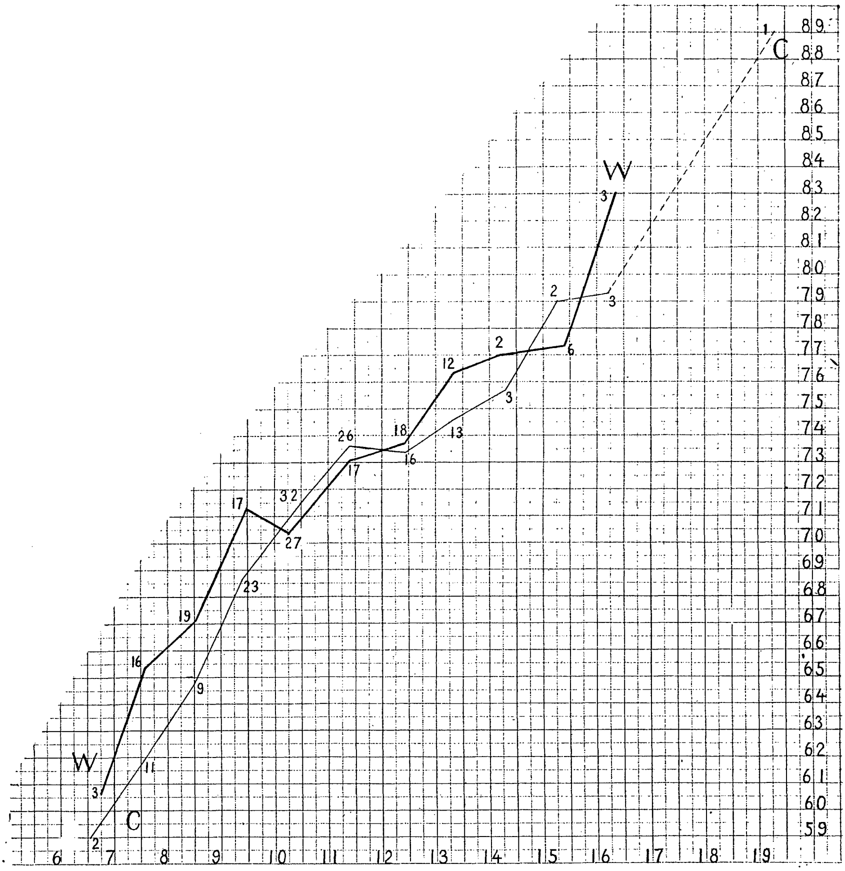

Fig. 1. Curves showing mean tail length in relation to the size of the animals. The heavier line (*W*) represents the condition in the offspring of warm-room parents, the lighter line (*C*) representing that in the offspring of cold-room parents. Abscissas denote weight in grams; ordinates denote tail length in millimeters. The figures along the curves denote the number of individuals in each size-group.

Finally, the chances that we shall obtain as high a proportion as nine out of ten[8] of the same sort are only 2 in 93.

It must be borne in mind, however, that we have the cumulative testimony of these three characters, all point-

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[8] The group in which the two contrasted lots showed an *equal* ear-length has been left out of account. This would correspond to the case of a coin remaining poised *edgewise*. In our probability estimates we have not contemplated such a contingency.

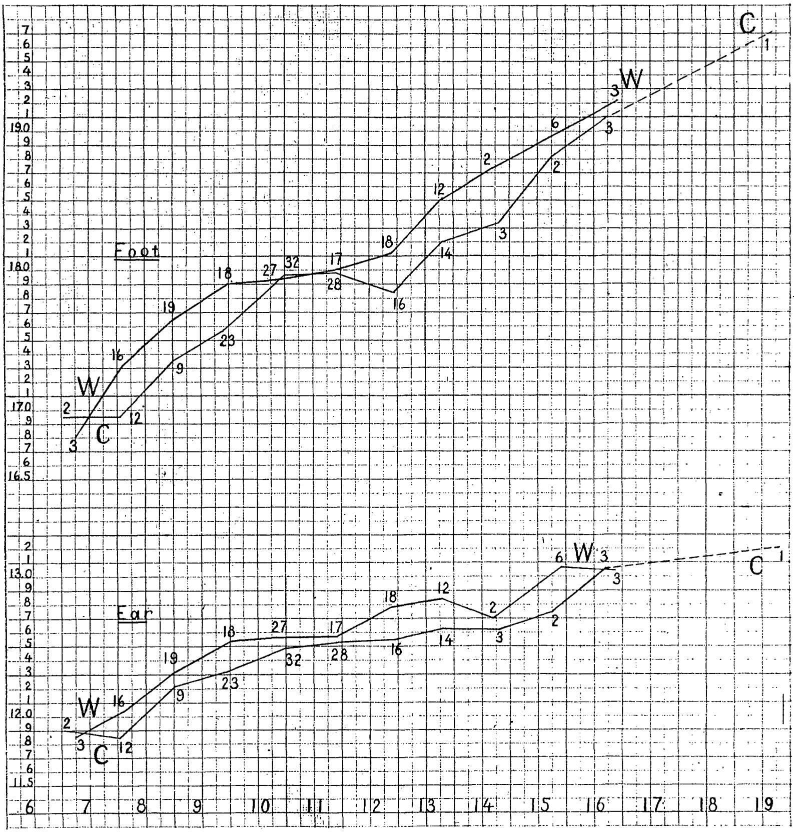

FIG. 2. Curves showing mean foot and ear length. The upper line (*W*) in each case is that showing condition in offspring of warm-room parents. For further explanation see Fig. 1.

ing in the same direction; *i. e.*, we have 26 out of 33 cases showing the same tendency. If we assume that these parts vary quite independently of one another,[9] and if we leave out of consideration the single case of equality, the probability of our obtaining such a large majority in a purely "accidental" way is only 1 in 1,869. In most of the practical affairs of life, we should reject such a contingency as not worth considering.

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[9] In reality, there is a certain degree of correlation between them, the extent of which has not been computed. This would render the chances somewhat greater than is here indicated.

Thus far, we have treated these groups as of equal value in our computations. From our table it will be seen, however, that the groups differ greatly in respect to the number of individuals comprised, and in respect to the magnitude of the differences shown. I have computed the probable errors of the averages for those seven groups which are large enough to make this worth while. Taking into account the three characters (tail, foot and ear) for the seven groups, we have, accordingly, twenty-one probable errors for each of the contrasted sets ("warm" and "cold"). A little figuring shows that in twelve of these twenty-one cases the difference between two contrasted averages is two or more times as great as the probable error of that difference; in one case the difference is over three times its probable error, and in three cases it is over four times its probable error.[10] The significance of these facts will be appreciated by any one familiar with statistical methods.

Diagrams (Fig. 1 and 2) have been constructed permitting of a comparison between the two contrasted sets of mice, with respect to the mean length of tail, foot and ear, for each of the size groups. These curves explain themselves, and further comment seems unnecessary.

The question naturally arises: How do these differences between the warm-room and the cold-room descendants compare in amount with the differences which were shown by the parents as a direct result of the external conditions? Unfortunately, the data necessary for a direct reply to this question are not at hand, since, in the case of the parents of this particular lot, foot and ear length were not determined at the age of six weeks. I have at hand, however, a set of measurements for a considerable number of mice (80 "cold" + 129 "warm"), which were subjected to substantially the same temperature conditions as were these parents. To determine the extent of the differences, we shall consider, not the differences between the gross averages, for reasons already stated, but the average difference, within each size group, between the "warm" and the "cold" figure. These mean differences, representing the extent of the modification shown at the age of six weeks by mice directly influenced by temperature are:

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[10] It is important to note that in none of the exceptional cases (*i. e.*, those in which the cold room descendants have *longer* peripheral parts) is the difference between the averages as high as two times its probable error. In one case it is practically equal; in another it is considerably less.

Tail	9.710 mm.
Foot	0.7138 mm.
Ear	0.2021 mm.

Corresponding figures for the warm-room and cold-room descendants with which we have been dealing are:

Tail	1.264 mm.
Foot	0.1890 mm.
Ear	0.1281 mm.

Comparing these two sets of figures, we find that the difference in tail length is 13 per cent. as great in the second case as in the first; the difference in foot length is 26 per cent. as great, while the difference in ear length is 63 per cent. as great! These figures are not offered as expressing, with even a rough degree of approximation, the proportional part of these parental modifications which is handed on to the offspring—even granting that such a transmission occurs. The relative magnitude of these three percentages is particularly surprising, in view of the fact that the tail is the organ which responds most decidedly to the temperature differences, while the ear has been shown to be least affected.[11] It might be argued that the very plasticity of a part, which makes it so responsive to outside influences, might render it correspondingly ill adapted to retaining such impressions permanently.[12] Such speculations are decidedly premature, however.

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[11] In my earlier paper I even expressed doubt as to the significance of those slight differences which I did find in the case of the ear. Further observations have, however, lessened these doubts.

[12] It must be pointed out that the tail is far more variable than either the foot or the ear.

Another set of measurements was made with this same lot of mice when they reached the age of three months. By that time the numbers had been considerably reduced by death. There were at the later date 114 of the cold-room descendants, and only 84 of the warm-room descendants. The survivors all appeared to be in good health, however.

In order to exclude the possible influence of suggestion or unconscious bias in determining these rather delicate caliper measurements, I adopted the plan of keeping myself in ignorance as to the parentage of each mouse until the latter had been measured.[13]

I shall not at present enter into as full an account of these later measurements as of the first series. The differences between the gross averages are even less to be relied upon here than in the case of the earlier figures, since the two contrasted lots differed much more in their mean size. The warm-room descendants were somewhat the heavier of the two, having a mean weight of 19.45 grams, as compared with 18.56 grams for the other lot. The body length was also somewhat greater for the former (87.683 mm.) than for the latter (86.703 mm.). For statistical purposes, the animals have been grouped in two different ways: (1) according to weight, as was done previously, and (2) according to body length.[14] The latter method of grouping seems a much fairer one than the first, for it is probable that the length of the appendages is correlated primarily with body length, and only incidentally with weight. The single weight-groups, it may be added, contained individuals which differed from one another by as much as 4 or 5 mm. of body length.

To consider the second of these methods first, the animals were divided into groups, within each of which the individuals differed by less than one millimeter in length. Of these groups there are 15 which allow of a comparison between cold-room and warm-room descendants. Now the "warm" figures for tail, foot and ear are larger than the "cold" figures in 12, 11 and 10 cases out of the 15, respectively. The chances for the "accidental" occurrence of such majorities (in either direction) are roughly 1 in 28, 2 in 17, and 3 in 10, respectively. The cumulative improbability, as regards the three cases, is very high, but the exact chances have not been computed.

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[13] The animals were put into separate small cages, each bearing an identification mark upon the bottom. These cages were "shuffled" by one or another of my colleagues in the laboratory.

[14] The mice were killed at the time of these later measurements. For this reason it was possible to determine the body length with accuracy. This is not feasible with living animals, even when etherized.

The results to be derived from a consideration of the weight groups need not be detailed here. It must be stated, however, that the figures, although showing the same general tendency as those we have considered, are not, in themselves, as convincing as were the earlier ones. Indeed, when the size groups are broken up into subgroups according to sex, the figures, for the males, at least, are somewhat equivocal.

Thus, while the results of these latter measurements on the whole confirm the results obtained earlier in life, they are not as striking as those, and, if taken by themselves, could not be regarded as demonstrative. This is due, in part, to the fact that we are dealing with smaller numbers of individuals. It is probably also due, in part, to the principle of the "leveling down of initial differences," concerning which I have had much to say in my earlier paper. And lastly, it is possible that unconscious bias in the use of the calipers may have somewhat exaggerated the differences shown in the earlier series of measurements, although caution was taken to avoid this.[15]

INTERPRETATION

Aside from delusion or deliberate prevarication on the part of the writer, several interpretations of these results seem theoretically possible.

[15] The caliper scale was at all times invisible to me until the points of the instrument were finally adjusted. Personally, I regard any such bias in making these measurements as improbable; but it can not be rejected as impossible.

1. The differences may be due merely to "coincidence" or "accident." The odds against such an occurrence have been shown to be high. Indeed the cumulative improbability that all of these differences have been accidental is enormous.

2. They might have resulted from a slight though constant biasing of the measurements in favor of that result which was calculated to give the greatest personal satisfaction. This possibility, which has already been considered, has been excluded in the case of the second series of measurements.

3. Granting their genuineness, the differences may be due, not to any specific influence (hereditary or otherwise) which has affected the tail, foot or ear directly, but to some general constitutional difference in the offspring of the two sets of parents. In other words, these differences in the length of the peripheral parts may be *correlated* with some constitutional difference of a very general sort. In this connection, it must be admitted that the offspring of the warm-room mice showed a very much higher mortality (40 per cent. between the first and second measurements) than those of the cold-room mice (20 per cent.). The former were likewise somewhat larger, on the average, when measured at the age of three months. Thus there did exist some sort of a constitutional difference. The possibility here considered can not, therefore, be set aside. On the other hand, there is absolutely no evidence in its favor.

4. An explanation closely similar to the last would be that the general stage of development in one lot of mice had been accelerated or retarded as compared with that of the other. We know that the ears and feet of young mice are relatively much larger than those of older ones. It might be contended, therefore, that the warm-room descendants were in a relatively more juvenile condition, despite the fact that they were, on the average, no smaller (*larger,* indeed, at the time of the later measurements).

Even this possibility can not be dismissed without a hearing.

5. The offspring themselves, during their fetal life, may have been influenced in some way by the differences of temperature to which the mothers were subjected during the first two weeks of pregnancy (see above). It is obvious, however, that in a warm-blooded animal, the fetus could not be directly affected by differences of temperature *as such.* It would be curious, indeed, if the parental modifications should be so closely paralleled under these circumstances.

6. The germ-cells of the parents may have been so affected by the external conditions to which the latter were subjected that modifications resulted in the offspring similar to those which were produced in the parents directly. This hypothesis has been invoked again and again to account for a certain class of facts which would seem at first sight to lend strong support to the Lamarckian hypothesis, *e. g.,* by Weismann and by Tower. Such an explanation could not, however, be applied in the present case without radical modification. For we may again point out that in a warm-blooded animal differences of temperature, *as such,* could not affect either the fetus or the germ-cells to any appreciable extent.[16] The suggestion might be made, however, that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Such a hypothesis can neither be proved nor disproved in the present state of our knowledge, but it is perhaps the type of explanation which is calculated to appeal most strongly to the biologist of to-day. It may be pointed out, however, that *if a mech-*

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[16] Pembrey (*Journal of Physiology,* Vol. XVIII, 1895, pp. 363–379) found the temperature of adult mice to remain constant at widely different external temperatures. In the young, however (under ten days old), the body temperature was found to vary with that of the atmosphere.

anism exists whereby the germ-cells may be so influenced as to bring about the parallel modification of parent and offspring, such a mechanism would be of exactly the same value for evolution as the "inheritance of acquired characters" in the old sense. For heredity, however, the case would be different. We should still be able to go on talking about the "continuity of the germ-plasm," though that expression would have been shorn of much of its meaning.

7. Finally, we have the view that the changes undergone by the parent body are in some way registered in the germ-cells, so as to be repeated, in a certain measure, in the body of the offspring. The "classical" attempt to make this process intelligible is of course Darwin's hypothesis of "pangenesis." Other views have been put forward recently[17] which are scarcely to be distinguished from the preceding type of explanation (no. 6).

It would not be profitable to enter into any scholastic discussion of these various hypotheses. One after another of these alternatives must be excluded by carefully planned experiments; and it is the intention of the present writer to continue such experiments on a much greater scale in the near future.

November 6, 1909.

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[17] *E. g.*, by Cunningham, Archiv für Entwicklungsmechanik, 1908.